15 Representation of Fat and Protein Gain at Low Levels of Growth and Improved Prediction of Variable Maintenance Requirement in a Ruminant Growth and Composition Model

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Abstract

We have refined a prediction system for ruminant animal growth and composition developed previously. The model represents body protein in two pools: viscera and non-viscera (muscle). Using sheep data-sets, we have simplified the adjustments in the model for protein gain and loss of body fat at near maintenance feeding, and more precisely estimated variable maintenance parameters. In the model, muscle and viscera each have an upper bound ($m^\star$ and $v^\star$, respectively). For muscle $m^\star$ is genetically fixed; however, $v^\star$ is affected by energy intake and muscle (protein) mass. Net energy intake above maintenance is used for muscle and viscera gain before its use for fat accretion. Our new work has allowed simplification of previous equations allowing gain of muscle or viscera at zero retained energy (RE) and for visceral growth. Maintenance energy includes a variable coefficient on body weight (BW) that results in a lag in change of maintenance requirements after intake changes. Alternatively, heat production may be represented by a regression equation with body protein components. Sheep growth and composition is more accurately predicted with the revised model, and the model predicts sheep empty BW (EBW) gain and fat content (± 25 g/day and 2.3% units respectively) more accurately than the current Australian feeding system. New additions refine predictions at levels of energy intake at or below maintenance.

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Introduction

Most current feeding systems predict RE in order to estimate growth rate by using some empirical relationship between RE and BW gain. Composition of growth may be inferred in some of these by assuming protein content of the fat-free mass and energy value of protein and fat gain (e.g. 22.01% of fat-free mass is protein and the energy contents of fat and protein gain are 39.6 and 23.8 MJ/kg respectively; NRC, 2000). The prediction of RE is derived from the feed not used for maintenance or other productive functions. This may be arrived at in different ways. In net energy systems it is:

$$NEG = (DMI - NEM_{req}/NEM_c)\,NEG_c$$

where NEG is net energy for gain (i.e. RE; kJ/day), DMI is dry matter intake (kg), NEM_{req} is net energy required for maintenance (kJ/day), and NEM_c and NEG_c are net energy concentrations (kJ/kg) in ration DM for maintenance and gain, respectively. In metabolizable energy (ME) systems it is:

$$NEG = (MEI - NEM_{req}/k_m)\,k_g$$

where MEI is ME intake (kJ/day), and k_m and k_g are efficiency of ME use for maintenance and gain, respectively. Alternatively, it may be expressed as:

$$NEG = MEI - HP$$

where HP is heat production (kJ/day). In the model described in this study, based on a set of models (Soboleva *et al*., 1999; Oltjen *et al*., 2000), we have chosen to predict growth using an estimate of RE as the driver in contrast to our earlier model, which used empirical relationships with the ratio of MEI to a reference MEI (Oltjen *et al*., 1986). Therefore, one of our objectives is to improve prediction of RE, essentially by estimating maintenance (which may be variable) or HP more accurately. This may require an estimate of visceral mass, since variation in maintenance and HP are greatly influenced by change in visceral organs such as gastrointestinal tract (GIT) and liver (Koong *et al*., 1982). Hence, in predicting composition of gain we separate growth into three pools: visceral and non-visceral protein and EB fat. Thus variable maintenance can be dynamically related to the protein pools in the model. Further, the current version of the growth model contains improved representations of growth at low or near maintenance levels. Previous versions (Soboleva *et al*., 1999; Oltjen *et al*., 2000) had unidentified parameters for visceral protein growth. Our objective is to illustrate the hypothesis tested, the methods used, and subsequent equations and parameters accepted in achieving more accurate visceral mass and variable maintenance predictions.

Description of Original Model

In the original dynamic model (Oltjen *et al*., 2000) viscera and non-viscera (muscle) each have an upper bound (v^* and m^* respectively). For muscle m^* is fixed, although the possibility of reaching this level depends on both the

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current intake and nutritional history of the animal. However, v^* is affected by energy intake and depends on previous nutrition. As in previous models (Oltjen *et al*., 1986) net energy intake above maintenance (NEG or RE) is used for viscera and muscle tissue gain before its use for fat accretion. Visceral tissues are more sensitive than muscle to changes in energy intake. Maintenance requirements and HP are related to MEI, but changes in maintenance requirements follow changes in intake with some time delay. This depends on both the magnitude and the duration of the change in energy intake. The model is expressed in terms of energy (kJ):

$$dm/dt = k_m(NEG + c_m f_a)(1 - m/m^*)$$

$$dv/dt = k_v(NEG + c_v f_a)(1 - v/v^*)^2$$

$$df/dt = NEG - dm/dt - dv/dt$$

where

$$v^* = cs_1\, MEI/(1 + cs_2 MEI)^2$$

$$\text{and } f_a = (1 - m/m^*)f/(f + f_0)$$

so that if energy intake is near maintenance, body protein can be gained and fat lost in the immature animal. Constants are k_m, k_v, c_m, c_v, cs_1, cs_2 and f_0. Note that k_m and k_v separate the RE into m or v, and are not partial energetic efficiencies. The EBW of the animal (kg) is connected to our state variables (m, v and f) by the relationship:

$$dEBW/dt = \left[(dm/dt + dv/dt)/(23,800 \times 0.2201)\right] + \left[(df/dt)/39,600)\right]$$

where 0.2201 is the protein content of the fat-free EB. The energy driving the growth of muscle and viscera is given by the term NEG:

$$NEG = MEI - HP$$

where HP is total heat production, i.e. the sum of HP for maintenance (HP_{maint}) and HP for gain (HP_{gain}). HP_{maint} is estimated as:

$$HP_{maint} = \alpha_t EBW^{0.75} + 0.09\, MEI$$

which is the form of Corbett *et al*. (1987) that partitions maintenance energy into that associated with metabolism and digestion of feed and

$$\alpha_t = \alpha_0\left[1 + b\,(MEI_t/MEI_0 - 1)(1 - e^{-t/\tau})\right]$$

results in a lag in change of maintenance requirements after intake changes from MEI_0 to MEI_t. Here b and τ are constants; MEI_0 and α_0 are original values of intake and maintenance coefficient, respectively. The HP_{gain} is:

$$HP_{gain} = MEI - HP_{maint} - NEG$$

If one assumes a constant efficiency of feed energy use for gain (k_{gain}):

$$NEG = k_{gain}(MEI - HP_{maint})$$

$$\text{or } HP = MEI - k_{gain}(MEI - HP_{maint})$$

Otherwise any general form for HP can be used.

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Values for the coefficients in the original model that were chosen empirically to fit Ferrell *et al*. (1986) are given in Table 15.1. Most parameters were well fitted, with the exception that c_v (–0.5 ± 0.7) in the equation allowing visceral growth at low RE was not identified. Also, simple correlation coefficients of the relationship between parameters (Oltjen *et al*., 2000) revealed strong relationships between c_m and f_0 (R^2 = 0.72), for example, and other parameters, suggesting that the equations allowing protein growth at near zero RE were overparameterized and should be simplified. The value of k_m was highly correlated (R^2 = 0.86) with fit of the model, suggesting great sensitivity to the partition of NEG to muscle. Also, Oltjen *et al*. (2000) suggested that systematic biases in model structure, more than parameter value estimation, needed further work.

Methods

Data obtained by Ferrell *et al*. (1986) studying compensatory growth of intact male Suffolk × Rambouillet × Finnish Landrace lambs were used to test model changes. Lambs were assigned to gain 16 (H), 5 (M) or –6 (L) kg during period one (42 days), followed by assignments of 27 (S), 16 (H), 5 (M) or –6 (L) kg gain during period two in an incomplete 3 × 4 factorial design with treatments HH, HM, HL, MH, MM, ML, LS, LH and LM (period one designated by first letter, period two by second). There were four lambs per treatment. Data for visceral protein alone were not available, so *v* has been defined as the sum of liver, heart, kidney, spleen and GIT protein, and *m* as the remaining EB protein for the example presented here. Measurements were made of the initial and final BW, average daily energy intake, and muscle, viscera and fat weight at slaughter. The dynamic system of three coupled

Table 15.1. Estimates of the parameters in the model of Soboleva *et al*. (1999) for sheep based on the data of Ferrell *et al*. (1986).

Parameter	Value	Standard deviation (SD)	Units
k_m	0.36	0.01	
k_v	0.56	0.02	
c_m	221	10	kJ/day
c_v	–0.5	0.7	kJ/day
*m**	351,200	1,086	kJ
cs_1	1.33	0.02	Day
cs_2	0.0000214	0.0000005	Day/kJ
f_0	12.3	2.5	kJ
b	0.117	0.006	
τ	48	5	Day
α_0	649	28	kJ/(day·kg$^{0.75}$)
k_{gain}	0.522	0.009	

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non-linear differential equations was solved numerically using initial conditions based on the BW of the animals at the beginning of the trial. We assumed that initial v (protein content) was 8.15% of BW, and that v was 16.58% of the sum of liver, heart, kidney, spleen and GIT weight. To account for the effect of the level of energy intake on maintenance requirements, the value of α_0 was adjusted relative to the HH treatment, and initial intake (MEI_0) was set to 19,000 kJ/day. The results from the simulation at day 84 were compared to the measurements made on the animals at this time.

Fitting the unknown parameters to the data is a simultaneous non-linear regression problem, given that the set of differential equations is solved numerically. The estimation involves simultaneous regression since the same parameters occur in each of the three equations. This means that the estimation must take account of both the different scales and variances between the three body components, and also the covariances between the residuals of these variables. For example, if fat had a greater variance than muscle or viscera, it would make the fat pool much more influential in determining the parameter values than muscle or viscera unless this greater variance were taken into account in the estimation.

The corollary of least squared parameter estimation for one equation is to minimize the determinant of the residuals for parameter estimation in simultaneous equations. This is also the maximum likelihood estimate when the residuals are multivariate normal. The derivation is given in Bates and Watts (1988).

Initially the parameter estimation was done by solving the set of differential equations numerically using a Runge–Kutta method with adaptive stepwise control (Press *et al*., 1989) and a continuous parameter genetic algorithm (Haupt and Haupt, 1998) to minimize the determinant of the residual covariance matrix of muscle, viscera and fat. These estimates were used as the starting values for estimation using the Markov Chain Monte Carlo method (Metropolis–Hastings algorithm; Tanner, 1996). This method also provided estimates of the parameter distributions.

Results

The model parameters c_m, c_v and f_0 allow body composition changes to occur at zero or low NEG. If we plot the best fit line through the component gains of m and f (Fig. 15.1, v lines were not significantly different from zero and are not shown), and specifically look at the graph near NEG of zero, we find that both m and f gain approach zero as maturity increases, but from different directions. Thus, young animals gain more protein and lose more fat than older ones when feeding is restricted to maintenance levels.

Since c_m and f_0 are highly correlated ($R^2 = 0.72$), we replaced the $f/(f + f_0)$ term in the f_a equation with a simple exponent on the $(1 - m/m^*)$ term:

$$f_a = (1 - m/m^*)^{e_2}$$

New estimates for c_m and e_2 are 1,340 kJ/day and 3.4 respectively. If we plot dm/dt at NEG = 0 for different m for the original and revised equations,

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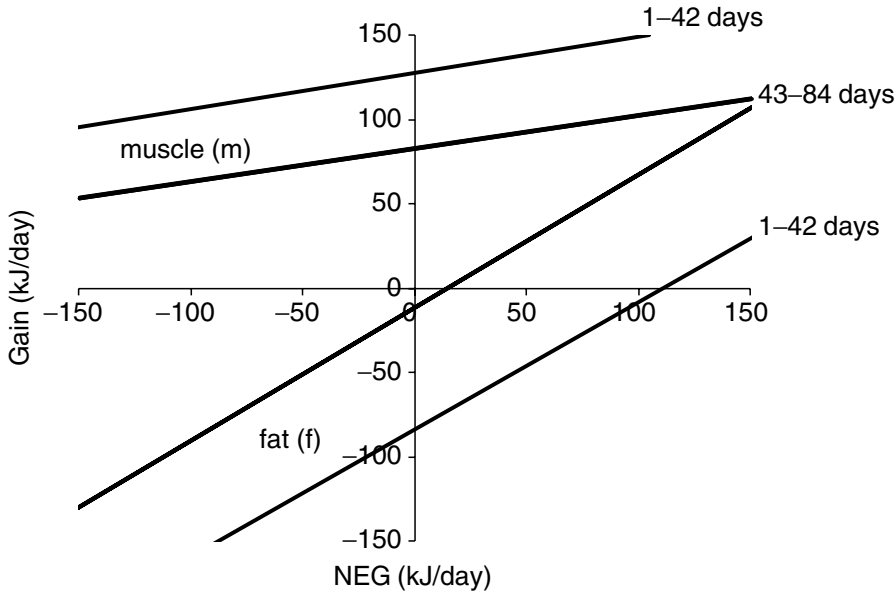

Fig. 15.1. Effects of age (period one, days 1–42; period two, days 43–84) on muscle or fat gain (loss) at near maintenance feeding levels (Ferrell *et al.*, 1986).

Fig. 15.2 shows that the original equation is not sensitive enough at younger ages, but the new form is more responsive. In fact, for animals of similar muscle mass, the previously assumed relationship that dm/dt increases more for relatively fatter animals was disproved in this data-set with a significant negative (not positive as expected) correlation (–0.69). Whether another equation form will be needed for long periods of maintenance feeding requires further data for analysis.

Turning next to viscera growth, if we assume that the calculation for v^* as a quadratic function of MEI is correct, f_a appears problematic. That is, when NEG is constrained to zero:

$$k_v c_v = (dv/dt)/(1 - v/v^*)2$$

and using average visceral values for the first and second 42-day periods, $k_v c_v$ is –872 and –3,803 respectively, but both values should be the same. The problem is that there is a decrease in v growth with maturity at similar NEG (Fig. 15.3).

Further, sensitivity analysis for the function v^* showed a significant ($P < 0.001$) correlation ($R^2 = 0.42$) between m and the residual viscera (predicted v^* minus observed v at the end of each period; Fig. 15.4).

Therefore, we refined the prediction of v^* using a data-set including longitudinal observations for viscera for rams and ewes held for long periods of time on constant intakes after various prior nutritional manipulations (Ball, 1996). An equation including both m and MEI best fitted the ram data (Fig. 15.5):

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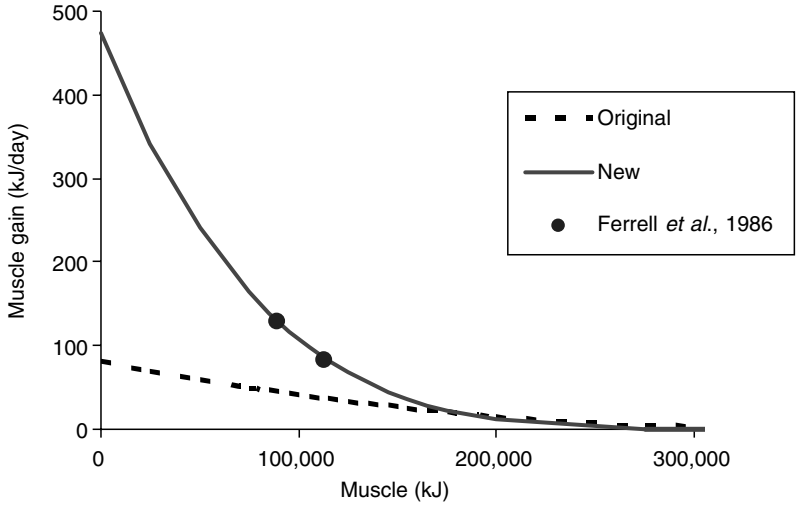

Fig. 15.2. Effects of age (increasing muscle, *m*) on rate of muscle gain at maintenance feeding; net energy for gain (NEG) = 0, for the original model with $f_a = [(1 - m/m^*)f/(f + f_0)]$ or a new model with an alternate equation form $f_a = (1 - m/m^*)^{e_2}$.

$$v^* = 0.31365\,\mathrm{MEI} + 0.041573\,m$$

without an intercept, since it was not significant ($P > 0.1$). When used with the Ferrell *et al*. (1986) data, similar good fit was observed (Fig. 15.6).

Simplifying the equation to predict visceral growth, we hypothesized that a simpler form might suffice, since fits of the previous equation were actually worse with NEG included:

$$dv/dt = k_v(v^* - v)^{e_3}$$

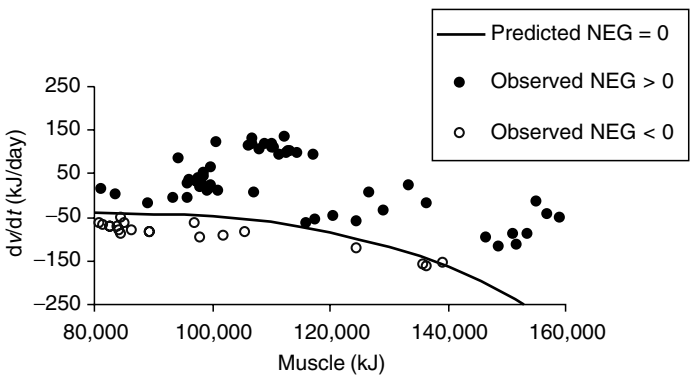

Fig. 15.3. Effects of age (increasing muscle, *m*) on rate of viscera gain around maintenance feeding; net energy for gain (NEG) = 0, for the original model.

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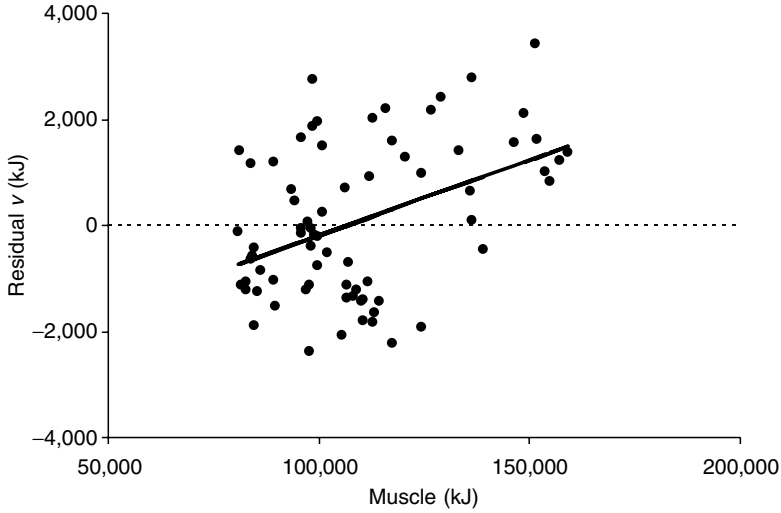

Fig. 15.4. The relationship of muscle (*m*) with residual viscera (predicted viscera, *v**, minus observed viscera, *v*) at the end of each period.

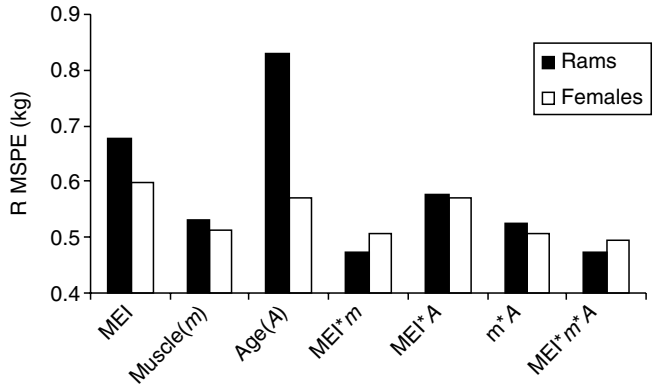

Fig. 15.5. Root mean square predicted error (RMSPE) of ending-period viscera mass for regressions with the terms metabolizable energy intake (MEI), muscle mass and age (Ball, 1996).

Fit of the Ball (1996) data-set for sheep both gaining or losing weight showed that e_3 was near unity and that k_v was 0.05 (Fig. 15.7).

Summarizing thus far, the new model gives:

$$dm/dt = k_m(NEG + c_m f_a)(1 - m/m^*)$$

$$dv/dt = k_v(v^* - v)$$

$$df/dt = NEG - dm/dt - dv/dt$$

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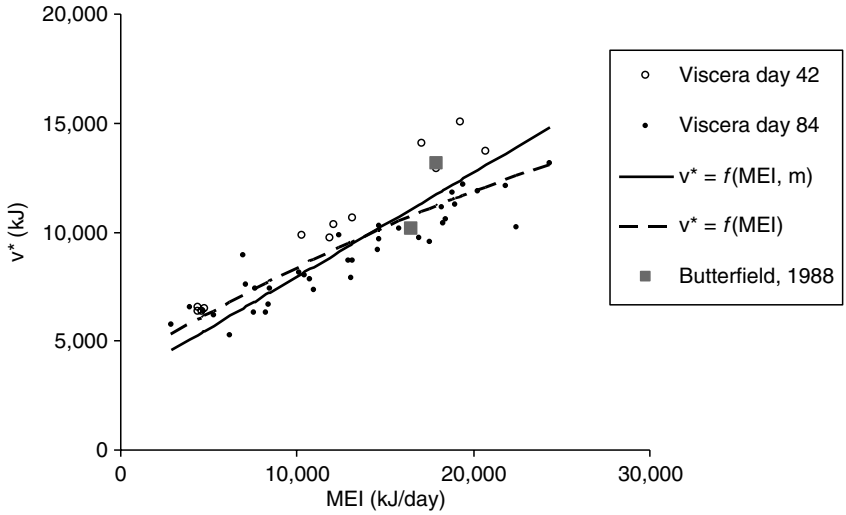

Fig. 15.6. Observed viscera at the end of each 42-day period (Ferrell *et al.*, 1986) and predicted v^* for the original equation based on metabolizable energy intake (MEI; Oltjen *et al.*, 2000) and a new equation based on MEI and muscle mass (m).

$$\text{with } f_a = (1 - m/m^*)^{e_2}$$

$$\text{and } v^* = cs_1 \text{MEI} + cs_2 m$$

where m is non-visceral EB protein (kJ), v is visceral EB protein (kJ), f is EB fat (kJ), NEG is RE (kJ/day), m^* is mature m, and k_m (0.353), c_m (1340 kJ/day), k_v (0.050/day), e_2 (3.4), cs_1 (0.314 day) and cs_2 (0.0416) are estimated parameters.

We also added the Standing Committee on Agriculture (SCA; 1990) energy terms for loss of body energy; for MEI < HP_{maint}, body energy is used at 0.8 efficiency, so:

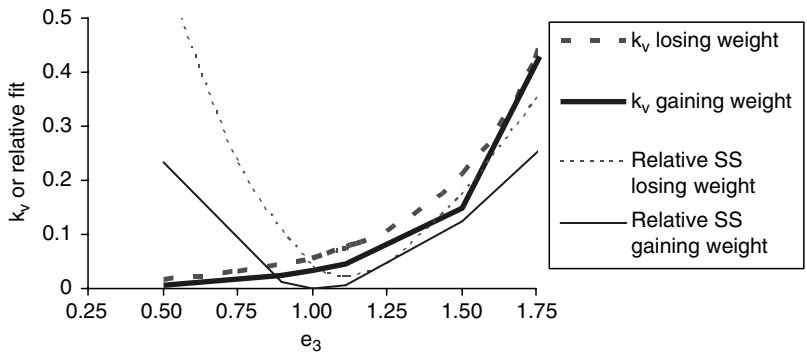

Fig. 15.7. Best fit for parameter k_v with different values of e_3 in the visceral growth equation and relative fit (sum of squared deviations, SS, between observed and predicted v) for the data of Ball (1996).

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$$HP_{maint} = \alpha_t EBW^{0.75} + 0.09 * MEI$$

$$\text{and } NEG = (K_{maint}/0.8)*(MEI - HP_{maint})$$

where K_{maint} = 0.02*M/D + 0.5 (SCA, 1990, p. 26, eq. 1.23); M/D is metabolizability of the feed.

Next we addressed a criticism that α_0 of 649 ± 28 kJ/(day·kg$^{0.75}$) was too large. If one again uses SCA (1990, p. 24, eq. 1.22) to estimate HP_{maint}:

$$HP_{maint} = KSM(260\, W^{0.75} e^{-0.03A})/k_m + 0.09MEI$$

$$HP_{maint} = 1 * 1.15 * 1 *(260 * 22.76^{0.75} e^{-0.03 * 0.33})/(0.02 * 10.6 + .5) + 0.09MEI$$

where K (species) is 1 for sheep, S (sex) is 1.15 for entire male, M (milk) is 1 for no milk feeding, W (weight, kg) is initial weight – 22.76 kg for Ferrell *et al*. (1986), A (age, max = 6 years) is initial age – 0.33 years for Ferrell *et al*. (1986), and k_m (kJ/kg) = 0.02M/D + 0.5 with M/D = 10.6. If we use W = 1.09(EBW + 2.9) as in SCA (1990, p. 40) or EBW of 17.98 kg:

$$HP_{maint} = 496\,EBW^{0.75} + 0.09\,MEI$$

for the initial conditions (Ferrell *et al*., 1986). Subsequent fits with NEG over the average period data have shown that k_{gain} and α_0 are highly correlated (r = 0.980; Fig. 15.8). We chose to fix k_{gain} as the SCA value of 0.4558 (k_{gain} = 0.043M/D; SCA, 1990, p. 49, eq. 1.39) and α_0 as 500 (actually 499.8 from fit; Fig. 15.8). Compare this 500 with 496 for SCA above, suggesting that SCA (1990) provides excellent fit for the average ram in the fitted data.

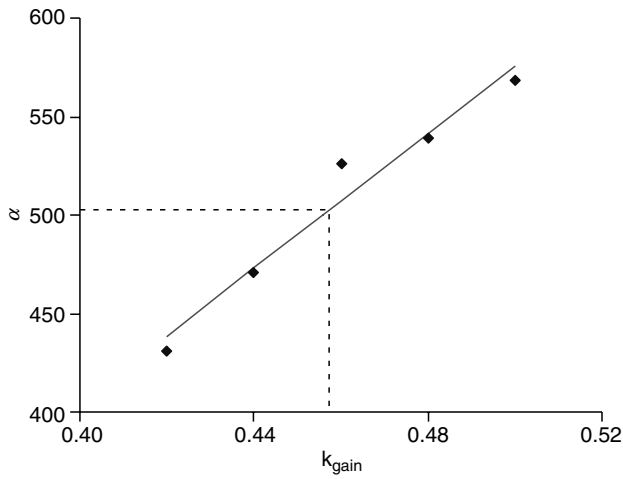

Fig. 15.8. Relationship between maintenance coefficient α at initial time and efficiency of metabolizable energy (ME) for gain (k_{gain}) for fits of retained energy (RE or NEG; Ferrell *et al*., 1986); dotted lines are for k_{gain} corresponding to ration fed (SCA, 1990).

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To this point we have used HP_{maint} as in the Australian feeding system (SCA, 1990) based on Corbett *et al*. (1987), but with a variable coefficient on BW:

$$HP_{maint} = \alpha_t EBW^{0.75} + 0.09\,MEI$$

$$\alpha_t = \alpha_0\left[1 + b(MEI_t/MEI_0 - 1)(1 - e^{-t/\tau})\right]$$

which results in a lag in change of maintenance requirements after intake changes from MEI_0 to MEI_t. Here EBW is empty body weight, t is time (days), b and τ are constants; MEI_0 and α_0 are original values of intake and the maintenance coefficient, respectively. Fit of the Nebraska data (Ferrell *et al*., 1986) shows that the double correction for variable maintenance is not necessary; the previously used coefficient on MEI, 0.09, is not different than zero in a model where α varies (Fig. 15.9).

Thus:

$$HP_{maint} = \alpha_t EBW^{0.75}$$

The next task is to determine the best values for the trajectory of α by estimating b and τ. Again fitting Ferrell *et al*. (1986), b and τ are related (r = 0.46; Fig. 15.10), and finding a unique value is not possible. Exploring the relative fit of the data parametrically (Fig. 15.11), there is an apparent plateau above b of 0.113 or τ of 25 days; the bottom is not defined except by zero, which is similar to fixed α. However, Fig. 15.9 demonstrates the advantage of a variable α. Thus, further research and additional longitudinal data are needed to estimate these parameters with precision. If we fix b (0.116) and τ (20.0 day), Fig. 15.12 illustrates the dynamic nature of variable maintenance. Overall, these changes significantly improve the prediction (Fig. 15.13) of body fatness (bias, –0.22, and standard deviation (SD), 2.29% units) and EBW gain (bias, 21, and SD, 25 g/day).

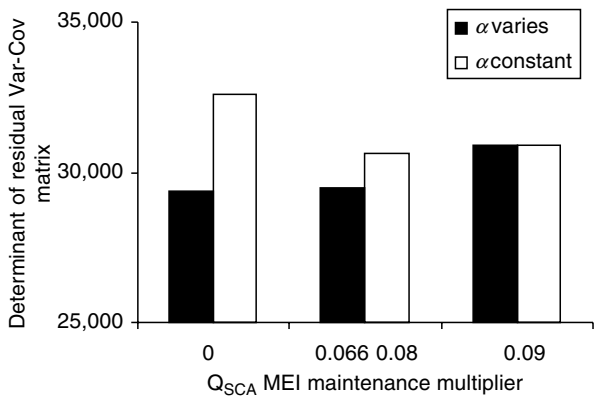

Fig. 15.9. Model fit of Ferrell *et al.* (1986) for $HP_{maint} = \alpha_t EBW^{0.75} + Q_{SCA}$ MEI, where Q_{SCA} is the SCA (1990) coefficient.

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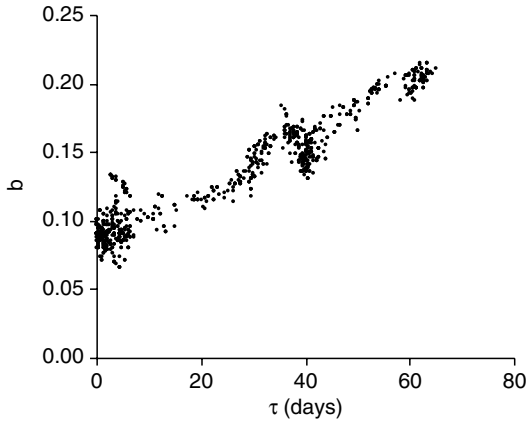

Fig. 15.10. Relationship between lag for maintenance, τ, and magnitude of maintenance adjustment, b, in fit of retained energy (RE or NEG; Ferrell *et al*., 1986).

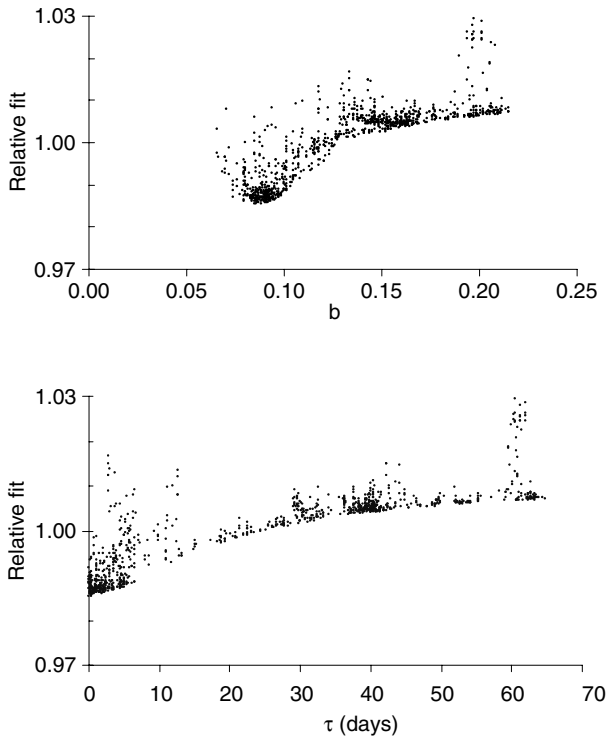

Fig. 15.11. Relative fit of retained energy (RE or NEG) for different values of maintenance adjustment, b, and lag for maintenance, τ (Ferrell *et al*., 1986).

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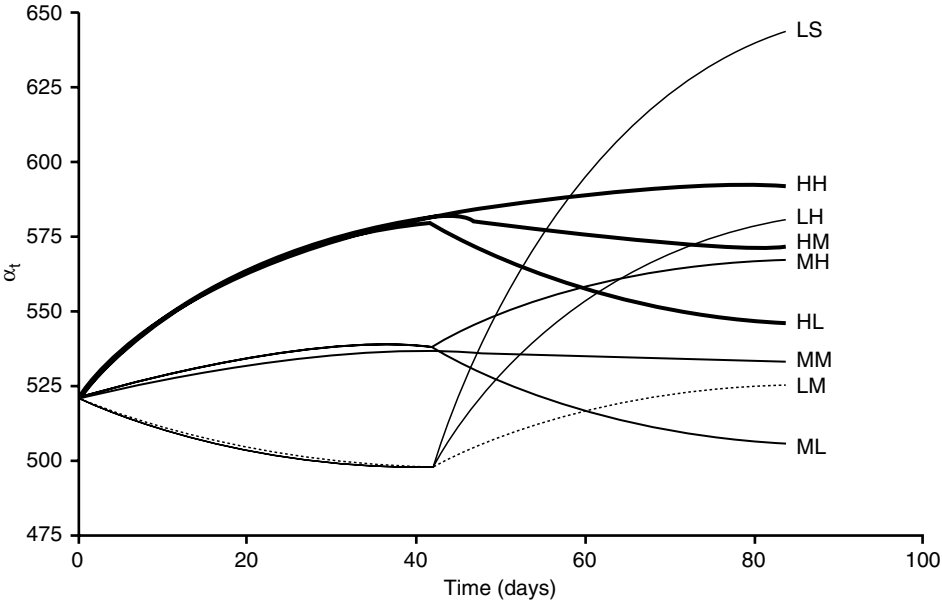

Fig. 15.12. Model-predicted maintenance coefficient (α) as a function of time (t) for nine treatment groups of Ferrell *et al*. (1986).

The maintenance function used is the traditional form adopted by nutritionists and may not be correct, especially in a dynamic situation. One of the advantages of the way the model is formulated is that the performance of different functions describing HP of the animal can be investigated. We tested different approaches to estimating HP and found that an alternative multiple regression equation including muscle protein, visceral protein, and the change in muscle and visceral protein could also be used (Fig. 15.14):

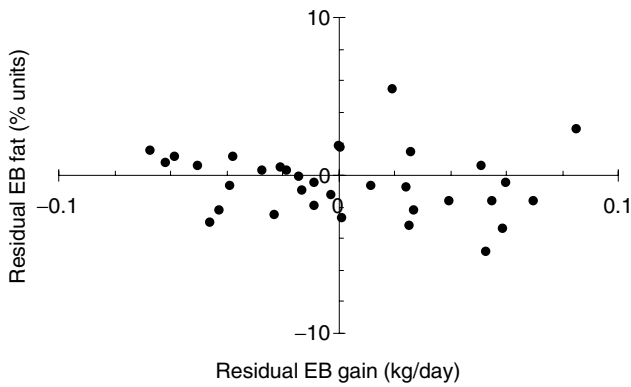

Fig. 15.13. Residual (predicted minus observed) empty body (EB) fat and gain for rams fed 84 days (Ferrell *et al.*, 1986).

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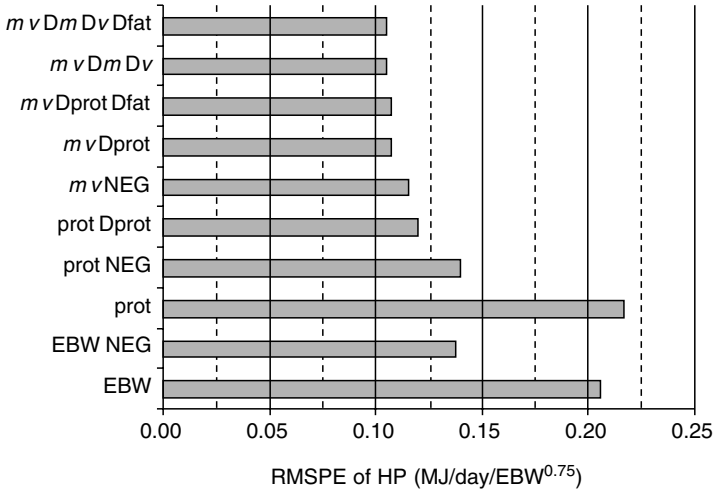

Fig. 15.14. Root mean square predicted error (RMSPE) of average daily heat production (HP) of rams (Ferrell *et al.*, 1986) using regression models with daily retained energy (RE or NEG), empty body weight (EBW) and EB and daily accretion (D) of muscle (*m*), viscera (*v*), fat and protein (prot).

$$HP = b_1 m + b_2 v + b_3 dm/dt + b_4 dv/dt$$

where b_1 and b_2 were 1.023±0.333 and 10.54±3.40 MJ/day/kg respectively, and b_3 and b_4 were 60.93±13.80 and 282.7±91.6 MJ/kg respectively (Oltjen and Sainz, 2001). The equation fitted the observed HP for rams (Ferrell *et al.*, 1986) in both periods (Fig. 15.15). HP per unit protein mass of viscera is

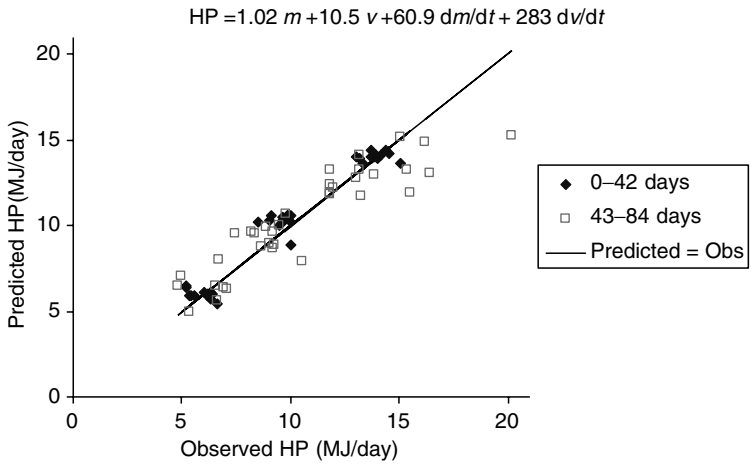

Fig. 15.15. Predicted and observed daily heat production (HP) for rams fed two 42-day periods (Ferrell *et al.*, 1986) using a regression model for muscle (*m*), viscera (*v*), and muscle and viscera daily gain.

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about ten times that of muscle. Eisemann *et al*. (1996) found that oxygen consumption of liver plus portal-drained viscera of 450 kg steers was about 7.5 times that of hindquarter tissues on a per unit mass basis. Also, since viscera responds faster than muscle to changing energy intake by the animal, this equation results in more dynamic HP. In any case either traditional net energy concepts or more general functions for HP can be compared to choose the best functional description.

Conclusions

Sheep growth and composition is more accurately predicted with the revised model, and the model predicts EBW and fat content more accurately than the current feeding system (SCA, 1990). New additions refine predictions at levels of energy intake at or below maintenance. Limitations identified are imprecise parameter estimates due to lack of longitudinal data-sets. The model provides the structure for predicting composition of growing cattle as well, but has yet to be completely parameterized and tested.

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